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Can Orchards Help Connect Mediterranean Ecosystems? Animal Movement Data Alter Conservation Priorities

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Abstract.—As natural habitats become fragmented by human activities, animals must increasingly move through human-dominated systems, particularly agricultural landscapes. Mapping areas important for animal movement has therefore become a key part of conservation planning. Models of landscape connectivity are often parameterized using expert opinion and seldom distinguish between the risks and barriers presented by different crop types. Recent research, however, suggests different crop types, such as row crops and orchards, differ in the degree to which they facilitate or impede species movements. Like many mammalian carnivores, bobcats (*Lynx rufus*) are sensitive to fragmentation and loss of connectivity between habitat patches. We investigated how distinguishing between different agricultural land covers might change conclusions about the relative conservation importance of different land uses in a Mediterranean ecosystem. Bobcats moved relatively quickly in row crops but relatively slowly in orchards, at rates similar to those in natural habitats of woodlands and scrub. We found that parameterizing a connectivity model using empirical data on bobcat movements in agricultural lands and other land covers, instead of parameterizing the model using habitat suitability indices based on expert opinion, altered locations of predicted animal movement routes. These results emphasize that differentiating between types of agriculture can alter conservation planning outcomes.

Introduction

As landscapes are converted to human uses, the resulting habitat loss and fragmentation hinder the ability of animals to move between remaining habitat patches (Noss 1987; Saunders, *et al.,* 1991; Rudnick *et al.,* 2012). This necessitates attention to conserving both remaining habitat patches and connectivity between them. In particular some wide-ranging species, such as mammalian carnivores, may need to move through human-dominated landscapes because of their large area requirements (Woodroffe & Ginsberg, 1998). But different land uses can facilitate or impede movement to different extents. For example use of agricultural lands by wildlife can differ considerably depending on crop type (Daily *et al.*,

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2003; Nogeire *et al.*, 2013), to the point that some crop types are barriers to movement whereas other types actually contribute to maintaining connectivity as wild habitat becomes more fragmented. Despite this variation in wildlife responses, the majority of connectivity assessments do not distinguish between types of agriculture (*e.g.*, Schadt *et al.*, 2002; Singleton *et al.*, 2002; Beier *et al.*, 2006; WHCWG, 2010; Castilho *et al.*, 2011; LaPoint *et al.*, 2013)

Connectivity assessments are often parameterized using expert opinion to score different land cover types as movement habitat, but these methods are increasingly criticized (Zeller, *et al.,* 2012). There is therefore a need for methods that can reliably estimate the resistance to movement posed by (difficulty of moving through) different land-cover types based on empirical data. Recent studies have demonstrated the utility of animal telemetry data for making inferences about the movement value of different land covers based on identified movement routes (Chetkiewicz, *et al.,* 2006; Richard & Armstrong 2010; Zeller, *et al.,* 2012; Reding, *et al.,* 2013; Tracey, *et al.,* 2013). Movement rates, rather than simple detections, reveal additional information about how animals experience a landscape; butterflies, pumas (*Puma concolor*), and other organisms tend to avoid moving into nonpreferred land-cover types and also move more quickly when traversing those land-cover types (Dickson, *et al.,* 2005; Kuefler, *et al.,* 2010). Using such movement behaviors to parameterize resistance surfaces for connectivity models can improve upon those based on detection data alone (Zeller, *et al.,* 2012; Reding, *et al.,* 2013).

Bobcats (*Lynx rufus*) in southern California present an opportunity to evaluate how empirical data can improve the ability of models to discriminate among the connectivity values of different land covers. Because bobcats are sensitive to urbanization and habitat fragmentation, they are a valuable indicator of landscape connectivity in this region (Crooks 2002; Riley, *et al.,* 2003; Riley 2006). Bobcats do, however, use human-dominated lands and can move through agricultural landscapes (*e.g.*, Hilty & Merenlender, 2004; Tucker *et al.,* 2008; Nogeire *et al.,* 2013). Avocado orchards in southern California have relatively high occupancy rates for bobcats (Nogeire, *et al.,* 2013) and may be important for bobcat movement as well. Habitat loss is particularly severe in California and other biologically rich Mediterranean-climate ecosystems (Mittermeier, *et al.,* 1998); this has spurred calls for conservation on private lands in Mediterranean ecosystems world-wide (Cox & Underwood, 2011).

We studied movement rates of bobcats fitted with global positioning system (GPS)-collars in relation to orchards and other land uses in a highly fragmented landscape containing a mix of agricultural, urban, and natural land cover types in southern California. We parameterized a connectivity model using these data and identified areas important for conserving bobcat movement through the study area. We then compared our connectivity model to one parameterized using a statewide habitat relationship system based on expert rating of bobcat habitat suitability to evaluate how empirical movement data such as ours can alter connectivity conservation efforts across a landscape where wildlands have been isolated by urban and agricultural development.

METHODS

STUDY AREA

Our study area was in Orange County, California and centered on the former Marine Corps Air Station El Toro (33°40′21.91″N, 117°40′39.54″W). Most of the base was purchased by private developers in 2005 with a portion proposed as a national wildlife refuge. We selected the study area because of its importance for both landscape connectivity and

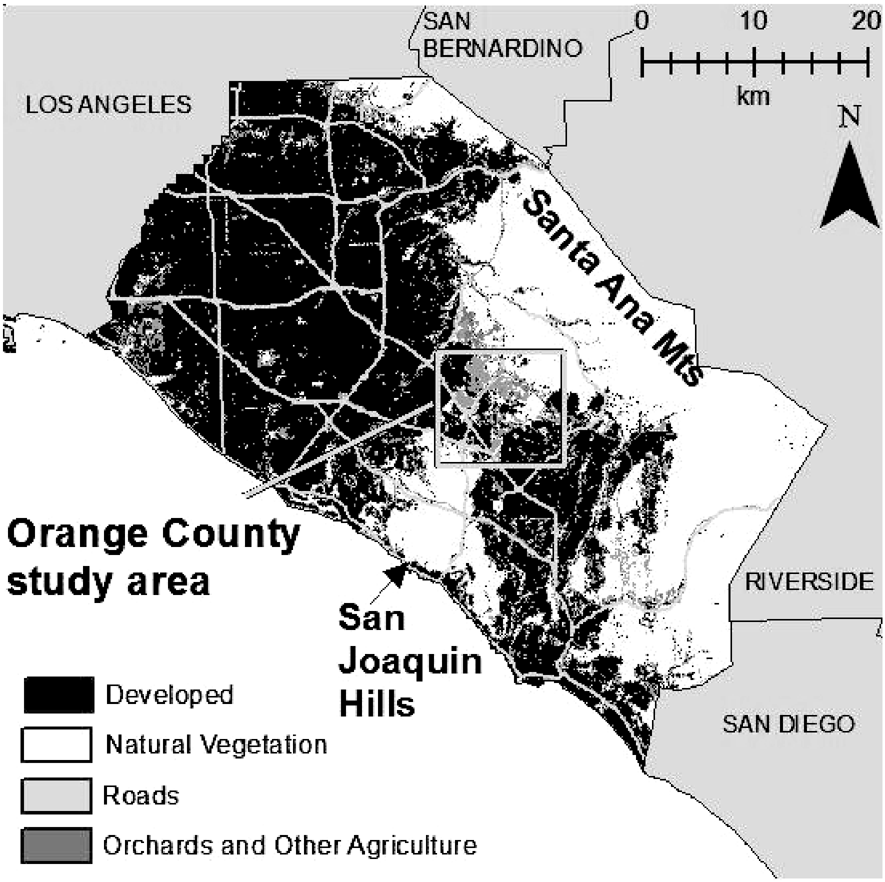

FIG. 1.—Study area within Orange County, California

agriculture; a 10 km wildlife corridor connecting the natural areas of the inland Santa Ana Mountains with the coastal San Joaquin Hills (Fig. 1) was recently proposed through the area (EcoSystems Restoration Associates, 2004; Orange County Great Park, 2011). The study area consisted of developed lands interspersed with shrub and grass vegetation, avocado orchards, row crops, and plant nurseries. Highway CA-241 separated our study area from the Limestone Canyon and Whiting Ranch Wilderness Parks: 2500 acres of sage scrub, chaparral, oak woodland, grassland and riparian habitat (Fig. 2).

LAND-COVER CLASSIFICATION

No single existing land cover map met our habitat mapping needs in terms of scale, accuracy, and land cover classes. We therefore created a land cover map using the National Land Cover Database (NLCD) (Homer *et al.*, 2004) and data from the 2005 Southern California Association of Governments (SCAG), California Department of Water Resources, and the California Avocado Commission. We used the NLCD land cover data to classify natural habitat types (scrub/shrub, grassland/herbaceous, and woodland) that were not identified in the SCAG layer. Lands classified as medium- to high-density developed by

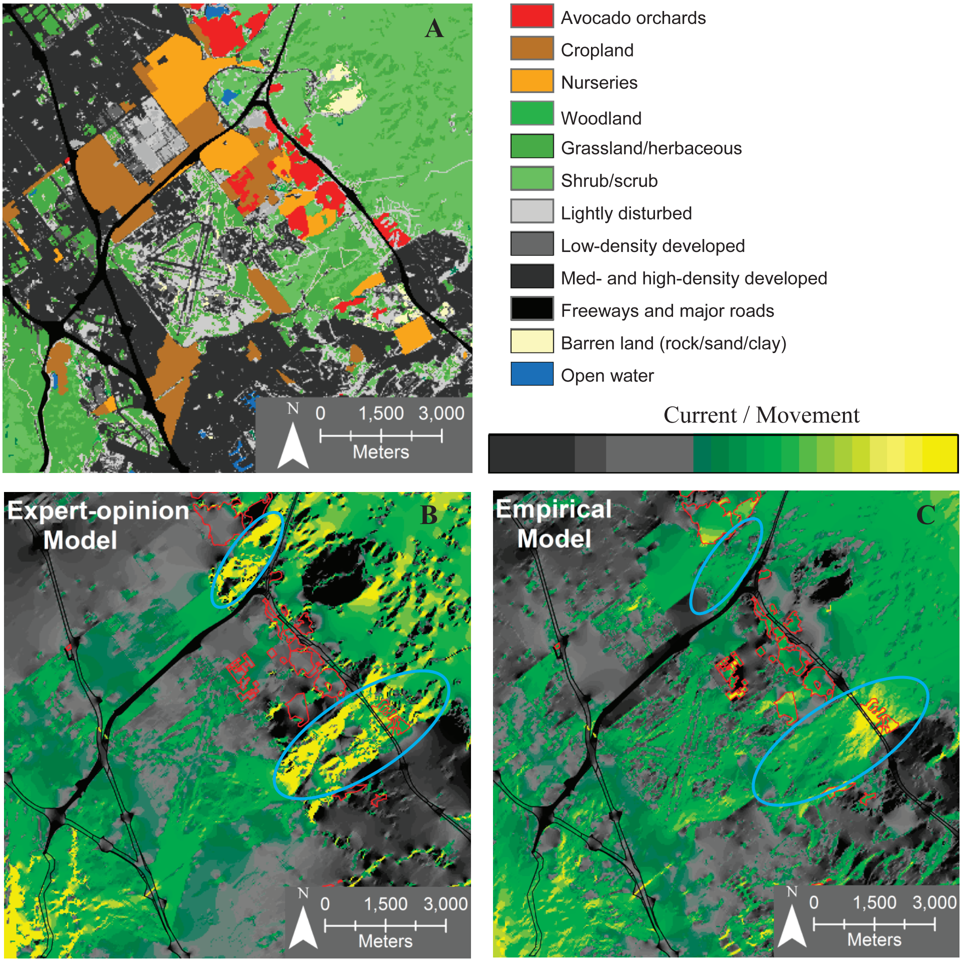

FIG. 2.—Results of connectivity modeling across the study region. The analyses used Circuitscape to assess movement between points in the Santa Ana Mountains and the San Joaquin hills in the upper right and lower left corners of the maps, respectively. Current values correspond to the modeled probability that a random walker moves through a given pixel when crossing the landscape. (**A**) Land-cover map of Orange County, California, study region for connectivity assessment. (**B**) Connectivity as modeled in the expert-opinion model (resistance values based on the California Wildlife Habitat Relationship database and literature). (**C**) Connectivity as modeled using the empirical model (resistance values based on measured movement rates). High current (yellow) indicates pinch points, where movement is funneled due to a lack of alternative pathways. Red polygons outline avocado orchards. Blue ovals show examples of pinch points where current is denser, and therefore movement is more concentrated, in the expert-opinion model. These pinch points are relieved by the additional pathways through avocado orchards (outlined in red) highlighted in the empirical model. In some cases, current flow is diverted by high-resistance row crops

either NLCD or SCAG retained those designations. Lands classified as low-density development or developed open space by NLCD or SCAG, and lands in classes that were essentially open space with substantial human activity (*e.g.*, school yards, golf courses, dirt roads, or urban parks), were then classified based on the extent of impervious surface:

TABLE 1.—Sources for land-cover data used to create base habitat map

Class	Source
Shrub/scrub	NLCD[1] land cover
Grassland/herbaceous	NLCD land cover
Woodland	NLCD land cover
Row crops	SCAG[2] or DWR[3]
Avocado orchards	SCAG, DWR, or CAC[4]
Nurseries	SCAG or DWR
Lightly disturbed	NLCD impervious surface
Low-density developed	NLCD impervious surface
Med-density developed	NLCD impervious surface
High-density developed	NLCD impervious surface
Barren land	SCAG
Roads and roadsides	SCAG

[1] National Land Cover Database 2001
[2] Southern California Association of Governments 2005
[3] Department of Water Resources 2005
[4] California Avocado Commission 2005

lightly disturbed (0-10% impervious surface), low-density developed (11-25% impervious surface), medium-density developed (26-40% impervious), and high-density developed (greater than 40% impervious). Lands classified as agricultural in the NLCD layer were further defined as avocado orchards, row crops, or plant nurseries by the SCAG and California Avocado Commission layers. When land-cover layers from the different sources were inconsistent, we verified classifications with ground visits or visual inspection of air photos (National Agriculture Imagery Program 2005, 1 m natural color). *See* Table 1 for source data on each land cover type and Figure 2 for the resulting land cover map.

BOBCAT MOVEMENT

We used GPS-telemetry data collected from four adult male bobcats with home ranges near orchards in Orange County to evaluate habitat use and differences in movement rates among land covers between Feb. 2007 and Apr. 2008. To capture bobcats we used wire cage traps (61x43x109 cm) with scent and dove lures, placed along washes, wildlife trails, and dirt roads near bobcat sign. One bobcat was incidentally captured by local animal control officers responding to a call for service. We restrained captured bobcats with an intramuscular injection of anesthesia (ketamine 10 mg/kg and xylazine HCL 1 mg/kg). Each bobcat was fitted with a collar with a GPS unit; Tellus (Lindesberg, Sweden) Basic collars weighed 270 g each and HABIT (Victoria, Canada) collars weighed 175 g each. After processing was complete, we antagonized the xylazine by administering an injection of yohimbine HCL (0.125 mg/kg body weight) and returned the animal to the cage trap. We monitored the bobcat until it recovered from the remaining anesthetic and then released it at its capture site. We programmed collars to collect coordinates at 15 min intervals during 3 h periods around the hours of 00:00, 06:00, 12:00, and 18:00. Two of the four collars also recorded information on position accuracy. Most of the positions had error estimates less than 50 m. Spatial accuracy of data from the other two collars (HABIT Research) was estimated from consultations with the manufacturer and inspection of the data. We excluded locations based on fewer than three satellites.

To quantify movement rates of bobcats, we created ''paths'' by drawing straight lines between each individual's locations in chronological order in a geographic information system (ArcGIS version 9.3; Environmental Systems Research Institute, Redlands, California). A single path was the line between a pair of consecutive points, and we limited our analyses to paths between points collected less than 35 min apart. We calculated the rate of bobcat movement as the distance between consecutive points for a GPS-collared individual divided by the time elapsed between the two points (m/min). If a path crossed two different land covers, it was counted as a sample in each land cover. For each land cover category, we considered the mean movement rate of all paths across all four animals. Movement rates were not calculated for open water or for road underpasses because we had no samples in these land covers.

Ethics statement: The Animal Care and Use Committees of the U.S. Geological Survey Western Ecological Research Center and Colorado State University (protocol #03-187A) approved animal handling and capture methods. Relevant permissions/permits for field research were obtained from California Department of Fish and Game, Orange County Great Park, and City of Irvine, California.

CONNECTIVITY ANALYSIS

We modeled connectivity for bobcats across the Orange County study area using Circuitscape version 3.5.7 (McRae & Shah, 2009). Circuitscape uses circuit theory to predict connectivity across a landscape in a way that incorporates all possible movement pathways, rather than the single, optimal pathway. The landscape is modeled as a conductive surface, with land-cover types assigned resistances proportional to the difficulty of movement through them. To model connectivity between source and target patches, 1 amp of current is injected into the landscape at the source and allowed to flow to the target patch, which is grounded. Circuitscape calculates effective resistance and densities of current flowing through intervening pixels. These can be used to measure overall connectivity between patches and movement probabilities through intervening pixels, and respectively reflect net movement probabilities through those pixels for random walkers moving from the source to the target patch (for details *see* McRae *et al.*, 2008). The model is particularly useful in highlighting areas where movement is constrained by landscape features and differentiating them from areas where multiple movement options exist (McRae *et al.*, 2008).

We compared two methods of estimating resistances of different landscape features: a habitat suitability model for bobcats based on expert opinion and an empirical model based on movement rates of the GPS-collared bobcats. We parameterized the expert-opinion model using habitat suitability values for bobcats from the California Wildlife Habitat Relationship database (CWHR) (CDFG 2008). We used the greater of feeding or cover suitability values in the CWHR database, and if more than one land-cover type in the CWHR corresponded to one of the land-cover classes, we used the average of the CWHR values (Table 2). The CWHR scored habitat values from 0-1, with higher values corresponding to more optimal habitat; we transformed these into resistances, with higher values corresponding to less optimal movement conditions using the formula:

$$Resistance = (1 - suitability) * 100$$

For land-cover classes not in the CWHR, we obtained resistance values from two sources: resistance values estimated by Singleton *et al.,* (2002) for forest-dwelling mammalian carnivores in the state of Washington and land-cover resistances estimated by Spencer *et al.,* (2010) for California, which were not species-specific. For impervious surface classes, we used resistances assigned to areas with high road densities and developed classes by Singleton *et al.*, (2002) and Spencer *et al.*, (2010), respectively.

TABLE 2.—Resistance values and movement rates for each land cover. Expert-opinion values derived from the California Wildlife Habitat Relationship (CWHR) database and from published literature. Empirical values based on bobcat movement rates. Movement rate is meters/minute, averaged across four animals

Class	Source of expert opinion	Expert-opinion model	Empirical model	Movement rate
Shrub/scrub	CWHR	3	11	7.25
Grassland/herbaceous	CWHR	34	21	8.54
Woodland	CWHR	36	1	5.84
Row crops	CWHR	45	75	15.58
Avocado orchards	CWHR	67	5	6.51
Nurseries	CWHR (open space)	78	21	8.52
Lightly disturbed	CWHR (open space)	78	14	7.67
Low-density developed	CWHR & published literature	85	39	10.96
Med-density developed	Published literature[1]	90	59	13.49
High-density developed	Published literature	90	66	14.50
Barren land	Published literature	70	100	18.86
Road underpasses	Half of non-road range of values	50	61	n/a
Roads and roadsides	WHCWG 2010	1000	1000	17.76

[1] Singleton *et al.*, 2002 and Spencer, *et al.*, 2010

For the empirical resistance model, we assigned resistance values proportional to the observed bobcat movement rates in different land-cover classes. We rescaled the movement rates between 0 and 100 for each land cover class i using the formula:

$$Resistance_i = \frac{v_i - v_{min}}{v_{max} - v_{min}} * 100$$

where v = movement rate = distance traveled / unit time, and v_{min} and v_{max} are the minimum and maximum movement rate over all land-cover categories, respectively. We retained original CWHR ratings for those land covers in which bobcats were not detected.

In both models we assigned major roads (including freeways and highways) a very high resistance value (1000). Because we did not have empirical data for roads, they received the same resistance value in both models and did not affect the comparison of the two methods. This high resistance value was used because freeways and major roads act as a substantial, although not complete, barrier to movement of bobcats (Riley *et al.*, 2006). Moreover, given major roads are only 2-3 pixels wide in most cases, modeled animals encounter roads only for a short distance. Road resistance values of similar magnitude were used for mammalian connectivity modeling by the Washington Wildlife Habitat Connectivity Working Group (2010). We assigned underpasses such as concrete culverts a resistance midway through the range of the resistances for all non-road land covers (Table 2).

For both models we analyzed connectivity between two natural areas, the Santa Ana Mountains and the San Joaquin Hills, by placing a source point in each area at least 5 km from the urban edge, approximately the SW and NE corners of Figure 2. We mapped Circuitscape current densities across the landscape (at a spatial resolution of 30 m) to identify and compare areas predicted to be important for connectivity under the expert-opinion and empirical resistance models.

RESULTS

Movement rate analyses were based on 8145 paths (4407, 2866, 757, and 115 for the four individuals). Movement rates of GPS-collared bobcats were lowest in orchards and natural land

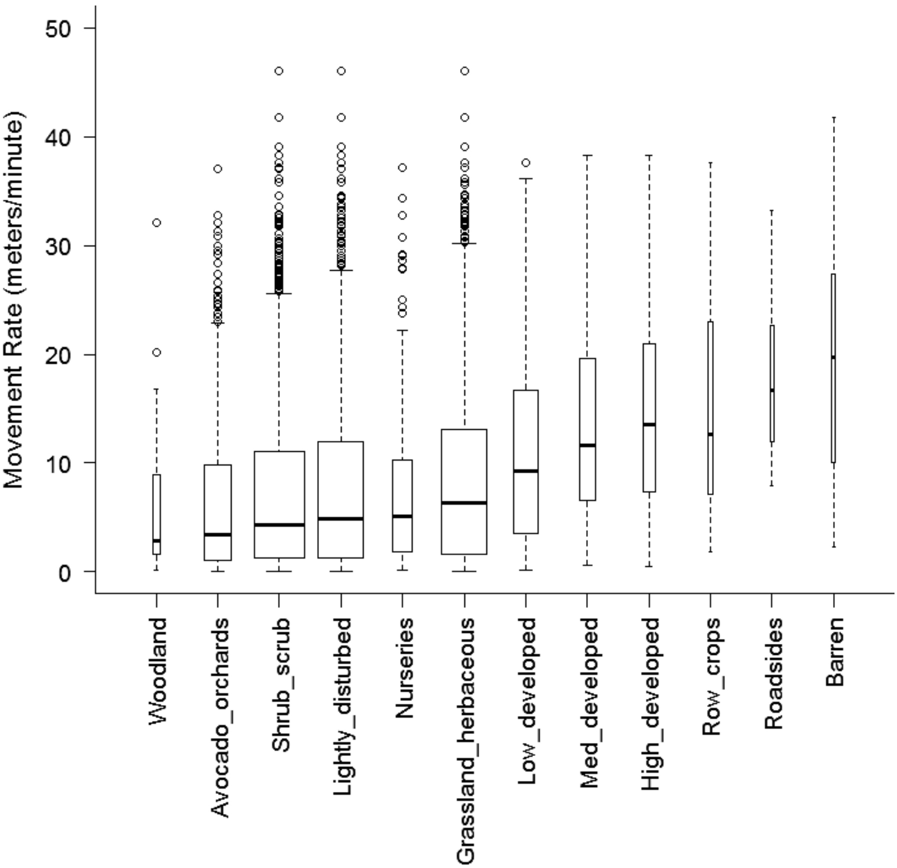

FIG. 3.—Movement rates of bobcats. Mean rate of movement (meters/minute) per land-cover type (N = 8145 paths, totaled over the 4 animals). Bars represent standard errors. Box widths are proportional to number of paths in each land-cover type, ranging from 16 paths (barren) to 2283 (shrub). The box marks the lower and upper quartiles and circles mark outliers

covers and greatest in row crops, high-density development, barren lands and roadsides (Fig. 3, Table 2). Rates of movement in lightly disturbed lands (0-10% impervious surface) were intermediate and somewhat less than in low-density development (11-25% impervious surface).

Predicted movement routes across the landscape differed between models parameterized using expert opinion and those based on empirical movement data (Fig. 2). In particular current flow patterns across the landscape were more constricted in the expert-opinion model (for example, in the blue ovals in Fig. 2) and more diffuse in the empirical model, reflecting additional pathways through orchards. Consistent with the empirical data on bobcat movement, current densities in orchards were greater in the model parameterized with these data. The total current summed across all avocado orchards (corresponding to the total net number of passages through avocado-occupied pixels; McRae *et al.*, 2008) was 2.8 times greater in the expert-opinion model versus the empirical model. Current densities in other land covers changed as well: for example, current densities in row crops were greater in the expert-opinion model than in the empirical model (Fig. 2).

DISCUSSION

Our findings that bobcat movement rates in avocado orchards were similar to those in natural land covers are in agreement with previous work using camera traps in a different study area showing some avocado orchards are frequented by bobcats (Nogeire, *et al.*, 2013); both studies suggest avocado orchards can provide important bobcat habitat. These orchards are also used by other carnivores (Dickson, *et al.*, 2005; Borchert, *et al.*, 2008; Nogeire, *et al.*, 2013) and could be important for their movement as well. Moreover, differentiating between orchards and other types of agriculture can change conservation priorities and improve conservation outcomes and efficiency.

These analyses also support previous work suggesting movement rates are a useful and relatively easy-to-measure metric which can contribute to parameterizing connectivity models (Dickson *et al.*, 2005; Chetkiewicz & Boyce, 2009). Dickson *et al.* (2005) also found close agreement between movement and compositional analyses for pumas in southern California in an area consisting of woodland, shrub/scrub, lightly disturbed, grassland, urban, and orchards. Moreover, for the five land covers in common between our studies, our rate rankings were identical to those for pumas except that woodland and scrubland were reversed. Movement rate data, however, should be interpreted carefully, considering differences in species' behavior and in each landscape and habitat type.

Movement rates may reflect habitat quality or potential risks encountered in different cover types (Zollner & Lima, 2004; Dickson, *et al.*, 2005). Typically, animals move more quickly through habitat with poor-quality resources or high probability of encountering risks (Kuefler *et al.*, 2010). In our study bobcat movement rates were highest in developed lands, and lowest in woodlands, avocado orchards, shrub/scrub, nurseries, and lightly disturbed lands. The rankings of favorable habitats inferred from movement rate data were similar to rankings of habitat preferences inferred from compositional analysis in the same habitat (Nogeire, 2011). Movement rates we recorded for bobcats in orchards, lightly disturbed lands, and in natural habitat types were also similar to those found for bobcats in the Tallahala Wildlife Management Area in Mississippi (6.15-8.15 m/min; Chamberlain *et al.*, 1999).

We emphasize our movement analyses were based on a limited sample size of four male bobcats. These results should not be generalized to all bobcats but rather illustrate how results can differ when using expert opinion versus movement rate data. Male and female bobcats differ in some aspects of habitat use. They have different home range sizes (Donovan *et al.*, 2011) and vary in their response to urbanization; males are more likely to incorporate urban development into their home ranges whereas females are more likely to avoid such areas (Tigas *et al.,* 2002; Riley *et al.,* 2003). Although we therefore might expect females to also respond differently to agricultural lands, Donovan *et al.,* (2011) found both male and female bobcats tended to avoid row crop agriculture. Further, in previous work, we documented female bobcats with kittens in avocado orchards (Nogeire *et al.,* 2013), suggesting females also use this land-cover type. Less is known about sex-related differences in felid movement. A study of bobcat movement rates in Mississippi found no difference between movement rates for males and females (Chamberlain *et al.,* 1999), and a study of puma movement rates and habitat selection in southern California also found similar rankings of land covers for males and females (Dickson *et al.,* 2005).

Our connectivity modeling results show how assumptions about the permeability of different agricultural types can influence conclusions relevant to conservation planning. The connectivity map derived from the expert-opinion model differed from the map based on empirical movement rates in the location and extent of areas of concentrated current flow, or ''pinch points,'' which would be expected to be especially important for connecting core habitat areas. In particular the more diffuse patterns in the empirical model indicate that animals moving through these parts of the landscape have more options and less constricted pathways because of the movement routes provided by avocado orchards. Therefore, classifying avocado orchards as poor-quality habitat or grouping them with row crops during connectivity modeling might produce misleading inferences about how connected a landscape is for a given species or lead to poor prioritization of lands to conserve connectivity.

Making effective conservation decisions, such as identification of lands for protection through purchase or conversion to easements or suitable locations for wildlife crossing structures across highways, will depend on well-supported models of habitat quality and landscape resistance (Beier *et al.,* 2008). A better understanding of how different agricultural types affect animal movement could also lead to entirely different conservation strategies. For example conservation easements to keep land in orchards could be a more cost-effective conservation strategy than outright purchase of natural lands.

Such strategies may be particularly useful in Mediterranean ecosystems, which harbor disproportionately high numbers of species, including nearly 3000 native vertebrates and over 48,000 native plants world-wide (Mittermeier *et al.,* 1998; Cox & Underwood, 2011) but which are also often heavily converted to human land uses. Cox and Underwood (2011) emphasize the conservation potential of those private lands which retain mostly natural vegetation, such as lands used primarily for grazing or timber harvest (Cox & Underwood, 2011). But our work also points to conservation opportunities in cultivated lands such as orchards. A full 23% of lands in California (30% across Mediterranean ecosystems globally) are in orchards, vineyards, or other cultivated lands. The value of cultivated lands for conservation will depend on the crop type, the location in the landscape relative to other habitats, and whether wildlife-friendly management practices are adopted. Orchards could facilitate conservation goals but not if they become population sinks where animals are more likely to be exposed to pesticides, vehicle collisions, or conflicts with humans.

More generally, despite concerns about the threats and efficiency of wildlife conservation in human-dominated lands (Phalan *et al.,* 2011; Packer *et al.,* 2013), there is growing interest in managing for movement of wild animals through agricultural areas (Muntifering *et al.,* 2006; Cosentino *et al.,* 2011). Our empirical and modeling results provide further evidence agricultural lands, in this case avocado orchards, have potential to contribute to conservation goals by providing habitat or facilitating connectivity between natural areas.

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